

# Detection and Evolution of Resistance to the Pyrethroid Cypermethrin in *Helicoverpa zea* (Lepidoptera: Noctuidae) Populations in Texas

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**ABSTRACT** The bollworm, *Helicoverpa zea* (Boddie), is a key pest of cotton in Texas. Bollworm populations are widely controlled with pyrethroid insecticides in cotton and exposed to pyrethroids in other major crops such as grain sorghum, corn, and soybeans. A statewide program that evaluated cypermethrin resistance in male bollworm populations using an adult vial test was conducted from 2003 to 2006 in the major cotton production regions of Texas. Estimated parameters from the most susceptible field population currently available (Burleson County, September 2005) were used to calculate resistance ratios and their statistical significance. Populations from several counties had statistically significant ( $P \leq 0.05$ ) resistance ratios for the  $LC_{50}$ , indicating that bollworm-resistant populations are widespread in Texas. The highest resistance ratios for the  $LC_{50}$  were observed for populations in Burleson County in 2000 and 2003, Nueces County in 2004, and Williamson and Uvalde Counties in 2005. These findings explain the observed pyrethroid control failures in various counties in Texas. Based on the assumption that resistance is caused by a single gene, the Hardy-Weinberg equilibrium formula was used for estimation of frequencies for the putative resistant allele ( $q$ ) using 3 and 10  $\mu\text{g}$ /vial as discriminatory dosages for susceptible and heterozygote resistant insects, respectively. The influence of migration on local levels of resistance was estimated by analysis of wind trajectories, which partially clarifies the rapid evolution of resistance to cypermethrin in bollworm populations. This approach could be used in evaluating resistance evolution in other migratory pests.

**KEY WORDS** *Helicoverpa zea*, pyrethroid resistance frequencies, adult vial bioassay, bollworm migration, cotton

The bollworm, *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae), is a polyphagous herbivore with >100 reported host plants (Kogan et al. 1978) and is one of the key pests of cotton and corn in the United States. Almost 74% of the U.S. cotton crop was infested with the budworm [*Heliothis virescens* (F.)]/bollworm complex in 2003 (Williams 2004) and 82.4% in 2005 (Williams 2006). This complex reduced the total cotton yield by 1.39% in 2003. No other pest caused >1% yield reduction in 2003 (Williams 2004). Across the U.S. cotton belt, these two species were the most damaging pests in cotton in 2005, with 95% of populations consisting of *H. zea*. In Texas, 2,105,156 ha were infested, representing 87% of the cotton crop, with a yield reduction of 2.13% (Williams 2006). In the United States, 520,778 cotton bales were lost because of bollworm and budworm, and 265,793 of these were

lost in Texas (Williams 2006). Cotton yield loss caused by the bollworm/budworm complex accounts for 22% of the total insect damage in the Texas High Plains (Parajulee et al. 2004), a 25-county production region that is the most concentrated area of cotton production in the world, accounting for 20% of U.S. cotton (Leser and Haldenby 1999). Economic infestations are frequently found in sorghum, soybeans, alfalfa, and other crops (Sparks 1981, Wolfenbarger et al. 1981, Luttrell et al. 1994).

The bollworm is a multivoltine species (King and Coleman 1989). Pupae overwinter in the soil and adults emerge in April–May. Most mating occurs within two to three nights of adult emergence, and egg-laying begins soon afterward. The entire life cycle can be completed in  $\approx 30$ –35 d (Bohmalk et al. 1982, King and Coleman 1989, Roberts and Douce 1999). The number of generations depends on the region, from four to five in Louisiana to perhaps seven in southern Texas (Sorensen and Baker 1983, Capinera 2001). Wind-aided displacement of migrating *H. zea* has been widely reported in the southcentral United States, where an atmospheric phenomenon known as the low-level, nocturnal wind jet frequently occurs. Migrating *H. zea* may concentrate at the altitude of the low-level jet, which significantly increases the moths'

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displacement rate (Wolf et al. 1986). An airborne radar tracked a putative "cloud" of migrating *H. zea* for 400 km from the Lower Rio Grande Valley of Texas to San Antonio, TX, in <8 h (Wolf et al. 1990). More recently, capture of *H. zea* marked with unique pollen has been associated with atmospheric transport of *H. zea* from distant sources of the pollen (Lingren et al. 1994, Westbrook et al. 1995a). Extensive radar observations indicate that long-distance *H. zea* migration frequently occurs in Texas (Wolf et al. 1986, Westbrook et al. 1998). Because of the bollworm's high reproductive rate and dispersal capabilities, isolated foci of resistance may cause a rapid spread of insecticide-resistant populations.

Pyrethroids are widely used in cotton against bollworm and other pests such as *Lygus* spp. (Snodgrass and Scott 2000) and stinkbugs (Snodgrass et al. 2005) because of their broad spectrum and cost effectiveness. Although the introduction of transgenic *Bt* (*Bacillus thuringiensis*) cotton in the United States has reduced the amount of insecticide applied for bollworm control (Edge et al. 2001), supplemental insecticide applications are needed for Bollgard (Monsanto Co. St. Louis, MO) cotton, expressing Cry1Ac, to prevent yield losses caused by bollworm (Gore et al. 2003a). Addition of pyrethroid oversprays to Bollgard II cotton, expressing stacked Cry1Ac and Cry2Ab, seems to be the best *Bt* toxin resistance management strategy currently available for bollworm (Jackson et al. 2004).

Since the early 1990s, various reports from Arkansas, Illinois, Texas, and Louisiana indicated that bollworm populations exhibited increased pyrethroid resistance (Abd-Elghafar et al. 1993, Kanga et al. 1996, Bagwell et al. 2000, Cook et al. 2003). During the mid- to late 1990s, resistance was characterized as a local phenomenon, and despite decreased susceptibility in bollworm populations, pyrethroids remained effective for its control in the mid-south, with no reports of field failures (Kanga et al. 1996, Bagwell et al. 2000). In Louisiana in 1995, no significant difference in response to pyrethroids was found between laboratory and field-collected *H. zea* strains, but in 1996, target site insensitivity was discovered in field-collected bollworms (Ottea and Holloway 1998). In South Carolina, a high level of resistance was detected in 1996 and 1997 (Brown et al. 1998). Concern about widespread resistance to pyrethroids in bollworm in the cotton belt generated interest in a multi-state monitoring program funded by the Insecticide Resistance Action Committee (IRAC) in 1998 and 1999 (Martin et al. 1999, 2000). The highest observed bollworm survivorship at 10  $\mu$ g cypermethrin/vial, the dosage accepted as discriminatory and lethal for heterozygote resistant moths, was observed in Alabama (4.9%) in 1998 and in South Carolina (25%) in 1999 (Martin et al. 1999, 2000), whereas for Texas, the highest survivorship at this concentration was 0.4% for 1998 (Martin et al. 1999) and 6% for 1999 (Martin et al. 2000). Follow-up studies on resistance to cypermethrin in bollworm populations from different Texas counties have been only preliminarily summarized (Pietrantonio et al. 2000,

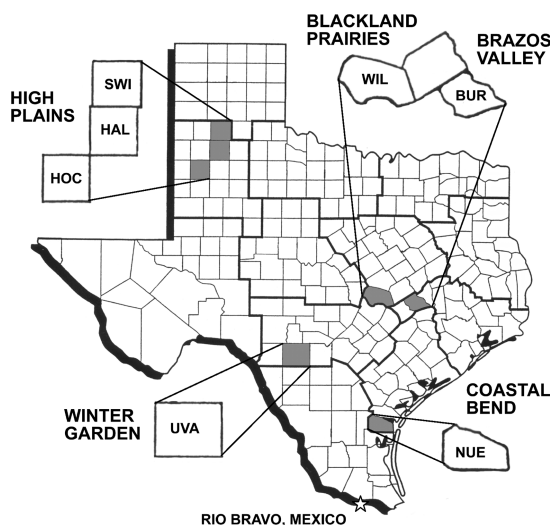


Fig. 1. Texas map showing the regions and counties where moths were collected and tested. Rio Bravo in Tamaulipas, Mexico, is located near the U.S.-Mexico border. BUR, Burleson Co.; HAL, Hale County; HOC, Hockley Co.; NUE, Nueces Co.; SWI, Swisher Co.; UVA, Uvalde Co.; WIL, Williamson Co. Thick lines on the map indicate the 12 Texas Cooperative Extension districts.

2004, 2005, 2006; Payne et al. 2001). The objective of this study was to investigate the current status, distribution, and evolution of cypermethrin resistance in bollworm populations in the ecologically diverse production regions of Texas, overlaying the analysis of wind trajectories relevant to migration.

## Materials and Methods

The cypermethrin resistance monitoring program was carried out from 2003 to 2006. Male moths of *H. zea* were trapped using the pheromone Hercon Luretape with Zealure (Great Lakes Integrated Pest Management, Vestaburg, MI) (Hartstack et al. 1979). Moths were collected in the morning, and only those with intact wing scales were used for adult vial tests (Plapp et al. 1987, Kanga and Plapp 1992). Vials were prepared in the Department of Entomology, Toxicology Laboratory at Texas A&M University, College Station, TX, and shipped to Texas Cooperative Extension collaborators and, in 2006, to Tamaulipas, Mexico. Control vials were coated with dehydrated acetone. Stock solutions were prepared with technical grade (95.2%) cypermethrin (FMC, Princeton, NJ) in dehydrated acetone for at least 48 h on 4-Å molecular sieves (EM Science, Gibbstown, NJ). Test vials of the following dosages were prepared: 0.15, 0.3, 0.6, 1, 1.5, 2.5, 3, 5, 10, 30, 60, and 100  $\mu$ g cypermethrin/vial. Vials with 60 and 100  $\mu$ g cypermethrin/vial were used in counties where moth survivorship at the 30- and 60- $\mu$ g/vial dosages, respectively, had been previously recorded. Vials with the 0.15- $\mu$ g cypermethrin/vial dosage were only prepared for the High Plains region.

**Table 1.** Brazos Valley, Burleson Co., cypermethrin bioassay for male bollworms collected from pheromone traps July 2000 and July 2003–2006

Date	<i>n</i> <sup>a</sup>	Slope ± SE	LC <sub>50</sub> <sup>b</sup> (95% CL)	LC <sub>90</sub> <sup>b</sup> (95% CL)	RR LC <sub>50</sub> (95% CI)	RR LC <sub>90</sub> (95% CI)	χ <sup>2</sup> (df)
Burleson <sup>c</sup>	400	1.47 ± 0.35	0.33 (0.08–0.59)	2.44 (1.51–5.76)	1	1	0.45 (3)
07/2000	250	1.70 ± 0.35	3.01 (1.49–4.99)	16.99 (9.52–50.96)	9.11* (3.41–24.29)	6.95* (2.72–17.75)	0.19 (3)
07/2003	554	1.76 ± 0.17	2.52 (1.98–3.12)	13.45 (9.93–20.41)	7.63* (3.29–17.70)	5.50* (2.80–10.82)	1.29 (4)
07/2004	360	2.04 ± 0.25	1.84 (1.32–2.39)	7.82 (5.81–11.85)	5.57* (2.36–13.18)	3.20* (1.63–6.26)	3.09 (4)
07/2005	400	2.15 ± 0.35	1.12 (0.82–1.43)	4.43 (3.16–7.91)	3.40* (1.45–7.98)	1.81 (0.88–3.71)	2.51 (3)
07/2006	200	3.39 ± 1.04	1.88 (0.98–2.43)	4.49 (3.38–10.73)	5.80* (2.37–13.70)	1.84 (0.91–3.72)	2.22 (5)

Resistance ratio (RR) with 95% CIs calculated by the method of Robertson and Preisler (1992). RR marked with \* indicate that LC are significantly different from susceptible population ( $P \leq 0.05$ ).

<sup>a</sup> Number of insects tested.

<sup>b</sup> Lethal concentration expressed in micrograms of insecticide per vial with 95% CL.

<sup>c</sup> Bioassay of Burleson County Sept. 2005 susceptible field population.

Collaborators conducted moth trapping and bioassays in their respective areas, following a protocol provided by the Toxicology Laboratory. One moth was placed in each vial, and the vials were stored at 27°C or at room temperature in areas where there was no access to an incubator. Equal numbers of moths were tested for each concentration. Mortality was evaluated after 24 h, and moths were categorized as alive, dead, or “knocked-down.” Moths that were alive but could not fly 2 m were considered knocked-down and were included as dead for calculations of percentage of mortality.

To estimate the statistical significance of cypermethrin resistance ratios for *H. zea* populations, it is imperative to determine the dosage response line (baseline) of a susceptible population. Unfortunately, the raw data for the bioassays of the susceptible population performed by Kanga et al. (1996) are no longer available. In cypermethrin response studies of *H. zea* conducted in Texas in 1988, 1989, and 1993, the 1988 field-susceptible population had a LC<sub>50</sub> of 0.05 µg/vial and a LC<sub>90</sub> of 0.57 µg/vial. In those same years, tolerance to cypermethrin was detected in field populations, with LC<sub>50</sub> values ranging from 0.09 to 0.44 µg/vial (Kanga et al. 1996). A Burleson County *H. zea* population evaluated in September of 2005 was the most susceptible of all tested that year and had a LC<sub>50</sub> = 0.33 µg/vial and LC<sub>90</sub> = 2.44 µg/vial, with no observed survivorship above the 3.0-µg/vial dosage. The estimated parameters of this Burleson Co. population are similar to those of susceptible field-collected

males of *H. zea* tested in 1992 in Missouri, with a LC<sub>50</sub> ranging from 0.3 to 0.96 µg/vial, having only 9% observed survivorship at the cypermethrin concentration of 2.5 µg/vial and 1% at the 5.0 µg/vial concentration (Knowles et al. 1993). Furthermore, the Burleson 2005 population was more susceptible than a laboratory “susceptible population” that we had previously obtained from the USDA-ARS, Southern Insect Management Research Unit, Stoneville, MS, as reference (Pietrantonio et al. 2006), and is comparable in response to the Texas field populations previously evaluated by Kanga et al. (1996). The estimated parameters of the Burleson Co. 2005 population support the assessment that a dosage of 2.5 µg/vial would kill all susceptible male moths (Kanga et al. 1996). The IRAC procedure used 5 µg/vial for the same discrimination in previous monitoring efforts (Payne et al. 2001), and 10 µg/vial is considered discriminatory for heterozygote resistant phenotypes. Because of the unavailability of a more susceptible laboratory colony, the estimated parameters of the Burleson Co. September 2005 population were used to estimate resistance ratios and their statistical significance for all populations.

Counties representing geographic regions included in these studies were Hockley and Hale/Smisher in the High Plains; Williamson in the Blackland Prairies; Burleson in the Brazos Valley; Uvalde in the Winter Garden; and Nueces in the Coastal Bend (Fig. 1). In 2006, monitoring was conducted in Rio Bravo, Tamaulipas, Mexico.

**Table 2.** Brazos Valley, Burleson Co., cypermethrin bioassay for male bollworms collected from pheromone traps 2006

Date	<i>n</i> <sup>a</sup>	Slope ± SE	LC <sub>50</sub> <sup>b</sup> (95% CL)	LC <sub>90</sub> <sup>b</sup> (95% CL)	RR LC <sub>50</sub> (95% CI)	RR LC <sub>90</sub> (95% CI)	χ <sup>2</sup> (df)
Burleson <sup>c</sup>	400	1.47 ± 0.35	0.33 (0.08–0.59)	2.44 (1.51–5.76)	1	1	0.45 (3)
04-21-06	187	2.37 ± 0.78	1.14 (0.22–1.81)	3.97 (2.65–11.62)	3.47* (1.21–9.90)	1.63 (0.75–3.50)	0.82 (4)
05-11-06	189	2.57 ± 0.57	1.32 (0.77–1.82)	4.17 (2.94–8.13)	4.01* (1.64–9.82)	1.70 (0.82–3.52)	2.27 (4)
06-09-06	299	2.05 ± 0.33	1.11 (0.74–1.47)	4.66 (3.35–8.00)	3.35* (1.40–8.03)	1.91 (0.94–3.86)	1.53 (5)
06-23-06	198	1.53 ± 0.32	0.99 (0.48–1.51)	6.80 (4.09–19.03)	2.99* (1.14–7.82)	2.78* (1.15–6.73)	2.36 (5)
07-21-06	200	3.39 ± 1.04	1.88 (0.98–2.43)	4.49 (3.38–10.73)	5.80* (2.37–13.70)	1.84 (0.91–3.72)	2.22 (5)
08-17-06	150	1.53 ± 0.45	0.56 (0.14–1.00)	3.88 (2.03–25.40)	1.71 (0.57–5.09)	1.58 (0.54–4.65)	3.30 (4)
09-07-06	250	2.68 ± 0.84	0.93 (0.29–1.34)	2.81 (2.60–14.42)	2.83* (1.08–7.43)	1.15 (0.56–2.35)	2.90 (4)

Resistance ratio (RR) with 95% CIs calculated by the method of Robertson and Preisler (1992). RR marked with \* indicate that LC are significantly different from susceptible population ( $P \leq 0.05$ ).

<sup>a</sup> Number of insects tested.

<sup>b</sup> Lethal concentration expressed in micrograms of insecticide per vial with 95% CL.

<sup>c</sup> Bioassay of Burleson County Sept. 2005 susceptible field population.

**Table 3.** Coastal Bend, Nueces Co., cypermethrin bioassay for male bollworms collected from pheromone traps, June/July 2003–2006

Date	<i>n</i> <sup>a</sup>	Slope ± SE	LC <sub>50</sub> <sup>b</sup> (95% CL)	LC <sub>90</sub> <sup>b</sup> (95% CL)	RR LC <sub>50</sub> (95% CI)	RR LC <sub>90</sub> (95% CI)	χ <sup>2</sup> (df)
Burleson <sup>c</sup>	400	1.47 ± 0.35	0.33 (0.08–0.59)	2.44 (1.51–5.76)	1	1	0.45 (3)
07/2003	340	1.44 ± 0.22	2.74 (1.69–4.08)	21.13 (12.59–49.08)	8.31* (3.33–20.75)	8.64* (3.65–20.45)	2.68 (3)
06/2004	360	1.65 ± 0.25	4.14 (2.88–5.66)	24.60 (15.76–51.39)	12.54* (5.23–30.03)	10.07* (4.52–22.40)	2.05 (4)
06–07/2005	400	1.46 ± 0.21	2.57 (1.70–3.61)	19.35 (12.16–40.70)	7.78* (3.19–18.93)	7.92* (3.51–17.86)	3.06 (5)
07/2006	200	1.82 ± 0.35	3.32 (2.41–4.86)	16.68 (9.46–54.98)	10.05* (4.19–24.09)	6.83* (2.60–17.91)	1.74 (4)

Resistance ratio (RR) with 95% CIs calculated by the method of Robertson and Preisler (1992). RR marked with \* indicate that LC are significantly different from susceptible population ( $P \leq 0.05$ ).

<sup>a</sup> Number of insects tested.

<sup>b</sup> Lethal concentration expressed in micrograms of insecticide per vial with 95% CL.

<sup>c</sup> Bioassay of Burleson County Sept. 2005 susceptible field population.

Data from all areas were sent to the Toxicology Laboratory at Texas A&M University for analysis. Data were analyzed using Polo PC Probit and Logic Analysis program (Russell et al. 1977) and dosage mortality regressions were plotted using SigmaPlot software. Data were corrected for mortality using the formula of Abbott (1925). Bioassays in some areas were conducted over several nights, and the data were pooled if probit lines from these populations were parallel and equal according to standard methodology (Robertson and Preisler 1992). The LC<sub>50</sub> and LC<sub>90</sub> values from the susceptible Burleson County September 2005 population were used to calculate resistance ratios (Tables 1–9). Confidence intervals (CIs) for resistance ratios were calculated as described in Robertson and Preisler (1992). The lethal concentration-resistant ratios were considered not significantly different if the 95% CIs included the number one (Robertson and Preisler 1992). This same methodology was also used to compare populations between different dates or locations, and thus, if the 95% CI included the number one, they were considered equal.

Calculation of bollworm resistance frequencies for the resistant allele ( $q$ ) was done using two formulas using the Hardy-Weinberg equilibrium formula (Falconer and McKay 1996). First, we based estimates of  $q$  from the percentage of putatively homozygote resistant insects ( $Q = q^2$ ) surviving the 10-μg/vial dosage, where  $q = \sqrt{Q}$ . Second, we estimated  $q$  as  $q = Q + 0.5H$ , based on the percentage of putatively homozygote resistant insects ( $Q$ ) and one half of the putatively heterozygotes ( $H = 2pq$ ) that survive either the 3- or 5-μg/vial dosage but not the 10 μg/vial, respectively, where  $q = q^2 +$

0.5(2pq). Assuming Mendelian segregation of a single allele, the frequency of the susceptible allele of the gene for resistance is  $p$  where  $1 = q + p$  (Plapp et al. 1990, Falconer and McKay 1996).  $\chi^2$  comparisons of  $q$  values between both methods ( $q = \sqrt{Q}$  or  $q = Q + 0.5H$ ) were performed for all populations using SPSS 14.0 (Shannon and Davenport 2001), and no statistically significant differences were detected ( $P \leq 0.05$ ), indicating that the number of homozygotes observed is the expected, based on the number of heterozygotes present in the population for a single allele model.

Analysis of wind trajectories was used to estimate bollworm migration patterns. We used the National Oceanic and Atmospheric Administration (NOAA) Hybrid Single-Particle Lagrangian Integrated Trajectory (HYSPLIT) model version 4.8 (Draxler and Rolph 2003, Rolph 2003) to generate wind trajectory maps for seven nights previous to the date on which vial assays were conducted at selected locations. Trajectories were calculated in the Real-time Environmental Applications and Display sYstem (READY) using the FNL data archive (hemispheric analysis of global data with 6-h forecast values replacing missing data), which covers both hemispheres of the globe at ≈191-km resolution. Backward trajectories (i.e., trajectories which terminated at a selected geographic destination) and forward trajectories (i.e., trajectories that originated from a selected geographic location) were generated. Lines on maps (Figs. 3–7) represent estimated 12-h nightly wind trajectories, arriving at, or originating at, 500 m above ground level (AGL), which is a representative altitude for bollworm migration in the southcentral United States (Lingren et

**Table 4.** Coastal Bend, Nueces Co. cypermethrin bioassay for male bollworms collected from pheromone traps, 2006

Date	<i>n</i> <sup>a</sup>	Slope ± SE	LC <sub>50</sub> <sup>b</sup> (95% CL)	LC <sub>90</sub> <sup>b</sup> (95% CL)	RR LC <sub>50</sub> (95% CI)	RR LC <sub>90</sub> (95% CI)	χ <sup>2</sup> (df)
Burleson <sup>c</sup>	400	1.47 ± 0.35	0.33 (0.08–0.59)	2.44 (1.51–5.76)	1	1	0.45 (3)
05/11–15/2006	370	3.16 ± 0.37	3.47 (2.95–4.12)	8.83 (6.95–12.61)	10.51* (4.60–24.04)	3.62* (1.90–6.88)	2.15 (3)
06/06–18/2006	600	2.09 ± 0.25	2.92 (2.31–3.55)	11.94 (9.08–17.88)	8.85* (3.83–20.43)	4.89* (2.52–9.47)	5.05 (6)
07/01–06/2006	200	1.82 ± 0.35	3.32 (2.41–4.86)	16.68 (9.46–54.98)	10.05* (4.19–24.09)	6.83* (2.60–17.91)	1.74 (4)
07/18–20/2006	280	2.30 ± 0.31	2.58 (2.09–3.20)	9.29 (6.66–15.83)	7.81* (3.38–18.04)	3.80* (1.87–7.72)	2.75 (5)
09/11–20/2006	300	1.78 ± 0.26	2.26 (1.64–3.08)	11.85 (7.61–24.50)	6.85* (2.88–16.29)	4.85* (2.18–10.78)	2.23 (3)
10/02–04/2006	140	1.10 ± 0.30	1.00 (0.34–1.73)	14.32 (6.09–189.06)	3.02* (1.06–8.57)	5.85* (1.45–23.59)	4.91 (5)

Resistance ratio (RR) with 95% CIs calculated by the method of Robertson and Preisler (1992). RR marked with \* indicate that LC are significantly different from susceptible population ( $P \leq 0.05$ ).

<sup>a</sup> Number of insects tested.

<sup>b</sup> Lethal concentration expressed in micrograms of insecticide per vial with 95% CL.

<sup>c</sup> Bioassay of Burleson County Sept. 2005 susceptible field population.



**Table 5.** Rio Bravo, Tamaulipas, Mexico, cypermethrin bioassay for male bollworms collected from pheromone traps, 2006

Date	<i>n</i> <sup>a</sup>	Slope ± SE	LC <sub>50</sub> <sup>b</sup> (95% CL)	LC <sub>90</sub> <sup>b</sup> (95% CL)	RR LC <sub>50</sub> (95% CI)	RR LC <sub>90</sub> (95% CI)	χ <sup>2</sup> (df)
Burleson <sup>c</sup>	400	1.47 ± 0.35	0.33 (0.08–0.59)	2.44 (1.51–5.76)	1	1	0.45 (3)
05/11/2006	100	3.03 ± 1.14	1.43 (0.73–2.02) <sup>d</sup>	3.79 (2.56–13.56) <sup>d</sup>	4.34* (1.71–10.99)	1.55 (0.64–3.76)	2.04 (3)
06/04/2006	100	1.13 ± 0.47	0.39 (0.02–0.80) <sup>d</sup>	5.31 (2.36–182.65) <sup>d</sup>	1.19 (0.27–5.22)	2.17 (0.44–10.65)	0.75 (3)
07/07–08/2006	200	1.79 ± 0.30	2.08 (1.50–2.83)	10.73 (6.69–25.51)	6.29* (2.65–14.95)	4.39* (1.89–10.19)	3.62 (5)

Resistance ratio (RR) with 95% CIs calculated by the method of Robertson and Preisler (1992). RR marked with \* indicate that LC are significantly different from susceptible population ( $P \leq 0.05$ ).

<sup>a</sup> Number of insects tested.

<sup>b</sup> Lethal concentration expressed in micrograms of insecticide per vial with 95% CL.

<sup>c</sup> Bioassay of Burleson County Sept. 2005 susceptible field population.

<sup>d</sup> For May and June only 90% CL could be estimated.

al. 1993, Westbrook et al. 1995b). Charts below the wind trajectory maps present vertical cross-sections for each of the estimated wind trajectories. The forward trajectories begin at 00 UTC (Universal Coordinated Time or Greenwich, UK, time; 2100 hours local time, beginning day) and end at 12 UTC (0900 hours local time, next morning). Backward trajectories begin at 12 UTC (0900 hours local time) and “end” at 00 UTC (2100 hours local time, beginning day; i.e., 12 h earlier). Although nights are shorter than 12 h during the summer, the 12-h duration helps to compensate for the moth flight speed, which is not included in these computations.

## Results

The  $\chi^2$  tests ( $\chi^2$  and  $P$  values) used to estimate how well the data fit the assumption of the probit model are presented in Tables 1–9. As the predicted values of the probit model did not differ significantly from the observed values in the vial assays (low  $\chi^2$  and  $P \leq 0.05$ ), the probit model was suitable for the concentration–response analyses. Based on the statistical analyses of the resistance ratios, there was significant variation in susceptibility among populations.

**Brazos Valley.** During all years in this study, Burleson and Nueces Counties (Fig. 1) were more intensively monitored for cypermethrin resistance, with more moths tested throughout the duration of the cotton growing season. Monitoring had been conducted from 1988 to 1993 and resumed in 1997 for the Brazos Valley. In June 1997 in Burleson Co. there was 8.3% (corrected) survivorship at the 3- $\mu$ g/vial concentration, and this increased to 13.5% toward the end of July (Pietrantonio, unpublished data). At the 10  $\mu$ g/vial concentration, survivorship varied from 1.5%

in mid-July to 2.7% in mid-August, putatively reflecting the percentage in pyrethroid resistant homozygote individuals. No survivorship at or above 30  $\mu$ g/vial was observed throughout the season. In 1998 there was no survivorship at the 10  $\mu$ g/vial concentration (P.V.P., unpublished data). In 1999, a high percentage survived the 3- $\mu$ g/vial concentration from a maximum of 19.2% in July to a minimum of 5.7% in September (Pietrantonio et al. 2000).

In Burleson Co., the most resistant population was detected in 2000, with a resistance ratio of 9.1 for the LC<sub>50</sub> and of 6.9 for the LC<sub>90</sub> (Table 1). From 2000 to 2005, Burleson Co. probit lines exhibited a progressive return toward susceptibility, but showed a statistically significant increase in the LC<sub>50</sub> for 2006 (Fig. 2). The level of resistance was significantly lower in 2005 (Table 1), with no resistance ratios reaching the value of five throughout the season (data not shown). In addition, no moths survived beyond the 3- $\mu$ g/vial dosage in July (Fig. 1). Equality tests (Robertson and Preisler 1992) showed that the probit line for July 2005 was significantly different ( $P \leq 0.05$ ) from those of July 2000, 2003, 2004, and 2006 (Fig. 2). Statistical analysis of LC<sub>50</sub> ratios for July 2005 versus all other years confirmed that all populations differed significantly from that of 2005 ( $P \leq 0.05$ ). Analysis of LC<sub>90</sub> ratios between the July 2005 population and those of July 2000, 2003, and 2004 confirmed that the ratios were significantly different ( $P \leq 0.05$ ), with the 2005 population being more susceptible. Only the LC<sub>90</sub> from July 2006 did not differ from that of July 2005 (Table 1).

The seasonal analysis of cypermethrin susceptibility for Burleson Co. during 2006 shows that a resistant population was only present during mid-season in late July, with a significant LC<sub>50</sub> resistance ratio of 5.8

**Table 6.** Blackland Prairies, Williamson Co., cypermethrin bioassay for male bollworms collected from pheromone traps, 2004–2005

Date	<i>n</i> <sup>a</sup>	Slope ± SE	LC <sub>50</sub> <sup>b</sup> (95% CL)	LC <sub>90</sub> <sup>b</sup> (95% CL)	RR LC <sub>50</sub> (95% CI)	RR LC <sub>90</sub> (95% CI)	χ <sup>2</sup> (df)
Burleson <sup>c</sup>	400	1.47 ± 0.35	0.33 (0.08–0.59)	2.44 (1.51–5.76)	1	1	0.45 (3)
June/July 2004	228	2.58 ± 0.51	2.53 (1.64–3.28)	7.95 (5.98–13.30)	7.66* (3.21–18.27)	3.25* (1.65–6.41)	1.09 (3)
July 2005	144	1.83 ± 0.38	4.68 (2.83–7.49)	23.49 (13.04–79.44)	14.18* (5.61–35.83)	9.62* (3.63–25.47)	3.47 (6)

Resistance ratio (RR) with 95% CIs calculated by the method of Robertson and Preisler (1992). RR marked with \* indicate that LC are significantly different from susceptible population ( $P \leq 0.05$ ).

<sup>a</sup> Number of insects tested.

<sup>b</sup> Lethal concentration expressed in micrograms of insecticide per vial with 95% CL.

<sup>c</sup> Bioassay of Burleson County Sept. 2005 susceptible field population.

**Table 7.** Winter Garden, Uvalde County, cypermethrin bioassay for male bollworms collected from pheromone traps, 2004–2005

Date	<i>n</i> <sup>a</sup>	Slope ± SE	LC <sub>50</sub> <sup>b</sup> (95% CL)	LC <sub>90</sub> <sup>b</sup> (95% CL)	RR LC <sub>50</sub> (95% CI)	RR LC <sub>90</sub> (95% CI)	χ <sup>2</sup> (df)
Burleson <sup>c</sup>	400	1.47 ± 0.35	0.33 (0.08–0.59)	2.44 (1.51–5.76)	1	1	0.45 (3)
Aug 2004	355	1.47 ± 0.24	1.39 (0.81–2.05)	10.21 (6.36–22.31)	4.20* (1.67–10.58)	4.18* (1.83–9.51)	2.00 (3)
July 2005	270	1.40 ± 0.26	2.36 (1.44–3.58)	19.38 (10.47–63.93)	7.15* (2.86–17.89)	7.93* (2.93–21.45)	1.46 (3)

Resistance ratio (RR) with 95% CIs calculated by the method of Robertson and Preisler (1992). RR marked with \* indicate that LC are significantly different from susceptible population ( $P \leq 0.05$ ).

<sup>a</sup> Number of insects tested.

<sup>b</sup> Lethal concentration expressed in micrograms of insecticide per vial with 95% CL.

<sup>c</sup> Bioassay of Burleson County Sept. 2005 susceptible field population.

(Table 2). LC<sub>50</sub> resistance ratios decreased from mid August until the end of the monitoring season, with the July LC<sub>50</sub> being significantly higher than those for August and September ( $P \leq 0.05$ ; Table 2). A trend of declining resistance ratios was observed from 2000 until 2005 for both the LC<sub>50</sub> and LC<sub>90</sub> resistance ratios (Table 1). The higher LC<sub>50</sub> resistance ratio of 5.8 for July 2006 in Burleson Co. was the exception (Table 2). It is also noteworthy that by the end of the 2006 season, the resistance ratio for the LC<sub>90</sub> was approximately one (Table 2), indicating that resistance levels were as low as the same time period in the previous year, 2005.

**Coastal Bend and Mexico.** In Nueces Co., the LC<sub>50</sub> and LC<sub>90</sub> resistance ratios were consistently high from 2003 to 2006 (Table 3). These are the highest values registered in Texas, and for the months of June or July, both ratios were significantly different ( $P \leq 0.05$ ) for all years (Table 3). A detailed analysis of the evolution of resistance in Nueces Co. for 2006 revealed that the LC<sub>50</sub> resistance ratios were high from early season in May and until September (Table 4). Most importantly from the control perspective is that the resistance ratios for the LC<sub>90</sub> remained high throughout the season (Table 4). It is significant that the field population in October 2006, after cotton harvest, remained significantly different from the reference population (Table 4). The high levels of pyrethroid resistance in early season indicated that resistant insects could be migrating from neighboring Mexico. Therefore, bioassays were conducted in 2006 in Rio Bravo, Tamaulipas, northern Mexico, at approximately the same time as those conducted in Nueces Co. (Table 5).

Early season bioassays in May revealed a LC<sub>50</sub> resistance ratio of 4.34 (statistically significant,  $P \leq 0.05$ ) in Rio Bravo, Mexico, with a not significantly different LC<sub>90</sub> resistance ratio (Table 5). June LC<sub>50</sub> values were not significantly different from those of the reference population, whereas resistance was detected in early July with LC<sub>50</sub> resistance ratio of 6.29 (Table 5). Statistical analysis comparing bioassays conducted on similar dates in Nueces Co. and Tamaulipas were conducted for May, June, and July data. In May, the Tamaulipas population was more susceptible than the Nueces Co. population (Tables 4 and 5) for both the LC<sub>50</sub> (95% CI for Nueces/Tamaulipas ratio = 1.49–3.94) and LC<sub>90</sub> (95% CI for Nueces/Tamaulipas ratio = 1.12–4.86). In June, the Tamaulipas population was also more susceptible than the Nueces Co. population (95% CI for LC<sub>50</sub> Nueces/Tamaulipas ratio = 2.06–26.79), but the LC<sub>90</sub> values did not differ (95% CI for LC<sub>90</sub> Nueces/Tamaulipas ratio = 0.48–10.52). For early July, the Tamaulipas population was marginally more susceptible than the Nueces Co. population (Tables 4 and 5; 95% CI for Nueces/Tamaulipas LC<sub>50</sub> ratio = 1.02–2.49), but the LC<sub>90</sub> values did not differ (95% CI for Nueces/Tamaulipas ratio = 0.58–4.18). Therefore, we hypothesized that the high levels of resistance detected in Nueces Co. early in the season were maintained locally with potential addition of migrant resistant insects from Mexico in July, at mid-season. However, analysis of wind trajectories considering Rio Bravo in Tamaulipas as a “source for bollworms” during the week beginning 1 July 2005, previous to the date of bioassays in July for Nueces Co.

**Table 8.** High Plains, Hockley Co. and Swisher Co., cypermethrin bioassay for male bollworms collected from pheromone traps, 2003, 2005, and 2006

Date	<i>n</i> <sup>a</sup>	Slope ± SE	LC <sub>50</sub> <sup>b</sup> (95% CL)	LC <sub>90</sub> <sup>b</sup> (95% CL)	RR LC <sub>50</sub> (95% CI)	RR LC <sub>90</sub> (95% CI)	χ <sup>2</sup> (df)
Burleson <sup>c</sup>	400	1.47 ± 0.35	0.33 (0.08–0.59)	2.44 (1.51–5.76)	1	1	0.45 (3)
08/2003	189	1.49 ± 0.26	0.94 (0.50–1.45)	6.86 (4.15–16.27)	2.87* (1.11–7.40)	2.80* (1.19–6.57)	0.62 (3)
Hockley Co.							
08/2005	360	0.89 ± 0.15	0.40 (0.18–0.65)	10.95 (5.69–37.87)	1.23 (0.45–3.37)	4.47* (1.59–12.57)	4.14 (6)
Hockley Co.							
07/2005	180	1.90 ± 0.47	0.81 (0.35–1.26)	3.86 (2.39–11.08)	2.46 (0.93–6.52)	1.58 (0.67–3.71)	1.19 (3)
Swisher Co.							
08/02–07/2006	300	0.91 ± 0.19	0.30 (0.10–0.55)	7.63 (3.64–35.92)	0.92 (0.30–2.77)	3.12 (0.98–9.85)	3.02 (5)
Hockley Co.							

Resistance ratio (RR) with 95% CIs calculated by the method of Robertson and Preisler (1992). RR marked with \* indicate that LC are significantly different from susceptible population ( $P \leq 0.05$ ).

<sup>a</sup> Number of insects tested.

<sup>b</sup> Lethal concentration expressed in micrograms of insecticide per vial with 95% CL.

<sup>c</sup> Bioassay of Burleson County Sept. 2005 susceptible field population.

**Table 9.** High Plains, Hockley Co. cypermethrin bioassay for male bollworms collected from pheromone traps, 2006

Date	n <sup>a</sup>	Slope $\pm$ SE	LC <sub>50</sub> <sup>b</sup> (95% CL)	LC <sub>90</sub> <sup>b</sup> (95% CL)	RR LC <sub>50</sub> (95% CI)	RR LC <sub>90</sub> (95% CI)	$\chi^2$ (df)
Burleson <sup>c</sup>	400	1.47 $\pm$ 0.35	0.33 (0.08–0.59)	2.44 (1.51–5.76)	1	1	0.45 (3)
06/27–28/2006	170	0.90 $\pm$ 0.26	0.15 (0.007–0.42)	4.013 (1.83–23.50)	0.46 (0.08–2.55)	1.64 (0.52–5.13)	4.55 (5)
07/11–16/2006	199	1.07 $\pm$ 0.23	0.17 (0.04–0.34)	2.81 (1.52–8.92)	0.54 (0.16–1.75)	1.15 (0.43–3.01)	0.35 (5)
08/02–07/2006	300	0.91 $\pm$ 0.19	0.30 (0.10–0.55)	7.63 (3.64–35.92)	0.92 (0.30–2.77)	3.12 (0.98–9.85)	3.02 (5)

Resistance ratio (RR) with 95% CIs calculated by the method of Robertson and Preisler (1992).

<sup>a</sup> Number of insects tested.

<sup>b</sup> Lethal concentration expressed in micrograms of insecticide per vial with 95% CL.

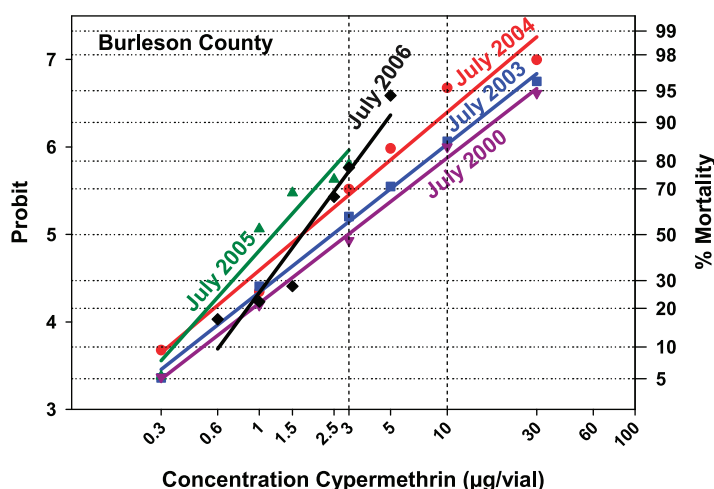
<sup>c</sup> Bioassay of Burleson County Sept. 2005 susceptible field population.

(Table 5), showed that potential bollworm trajectories were directed toward the northwest and not toward Nueces Co. (Fig. 3). Similar trajectories were observed earlier in the season for the weeks of 5–11 May and 1–7 June (data not shown). Therefore, wind trajectories do not support the hypothesis that resistant moths in Nueces Co. at mid-season originated in Rio Bravo, Tamaulipas.

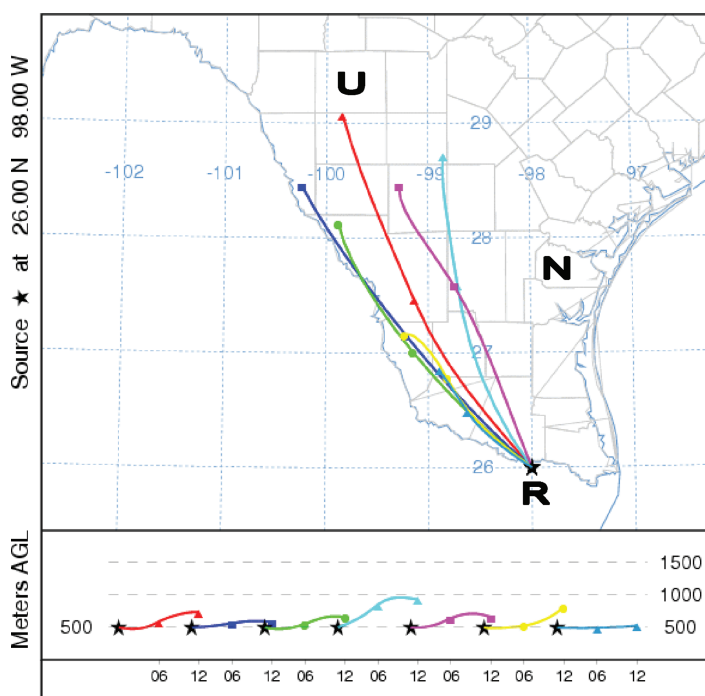
**Blackland Prairies.** The data on cypermethrin resistance for Williamson Co. are shown in Table 6. Williamson Co. is separated geographically from Burleson Co. only by Milam Co. (Fig. 1). During 2004, the resistance ratios were similar between Burleson (Table 1) and Williamson Co. populations (Table 6). However, the resistance ratios increased in Williamson Co. during July 2005, when both populations had significantly different LC<sub>50</sub> values (Tables 1 and 6; 95% CI for LC<sub>50</sub> Williamson/Burleson ratios = 2.4–7.03) and LC<sub>90</sub> values (95% CI for LC<sub>90</sub> Williamson/Burleson ratios = 2.16–12.96). Additionally, the July probit lines from 2003 to 2005 for Williamson Co. were parallel but significantly different (data not shown), showing a progressive and rapid evolution toward high frequency of resistant individuals in 2005 (Pietrantonio et al. 2006).

A comparison of July 2005 LC<sub>50</sub> resistance ratios for Williamson and Nueces Counties populations may suggest that resistance was higher in Williamson Co. (Tables 3 and 6). However, the LC<sub>50</sub> values were only marginally significantly different because of the lower numbers of insects tested for Williamson Co. in July 2005 (Table 6), and consequently, a wider range in the confidence limits for this LC<sub>50</sub> (95% CI for LC<sub>50</sub> Williamson/Nueces ratio = 1.018–3.21). Furthermore, the LC<sub>90</sub> values were not different between populations (95% CI for LC<sub>90</sub> resistance ratio Williamson/Nueces = 0.45–3.21).

The significant differences in bollworm population resistance ratios between Burleson (Table 1) and Williamson (Table 6) Counties in 2005, which are geographically close (Fig. 1), motivated the consideration of differential migration of resistant alleles as a factor that could explain the higher resistance ratios in Williamson Co. Therefore, a reverse analysis of wind trajectories considering Williamson Co. as the “destination” (backward trajectory) was conducted in July 2005, encompassing the week previous to the date the bioassay was performed in Williamson Co. This showed that several trajectories from Nueces Co. converged toward Williamson Co. during those dates



**Fig. 2.** Probit analysis for male bollworm field-collected during mid season in 2000 and 2003–2006 in Burleson County (Brazos Valley) and exposed to cypermethrin coated vials for 24 h. Lines are statistically parallel but not equal ( $P \leq 0.05$ ). The probit line for 2005 is significantly different from those of 2000 and 2003–2006. The dotted vertical lines indicate the discriminatory doses for susceptible moths ( $<3 \mu\text{g}$  cypermethrin/vial) and heterozygote resistant moths ( $<10 \mu\text{g}$  cypermethrin/vial). Notice that in July 2000, about one half of the population was resistant.





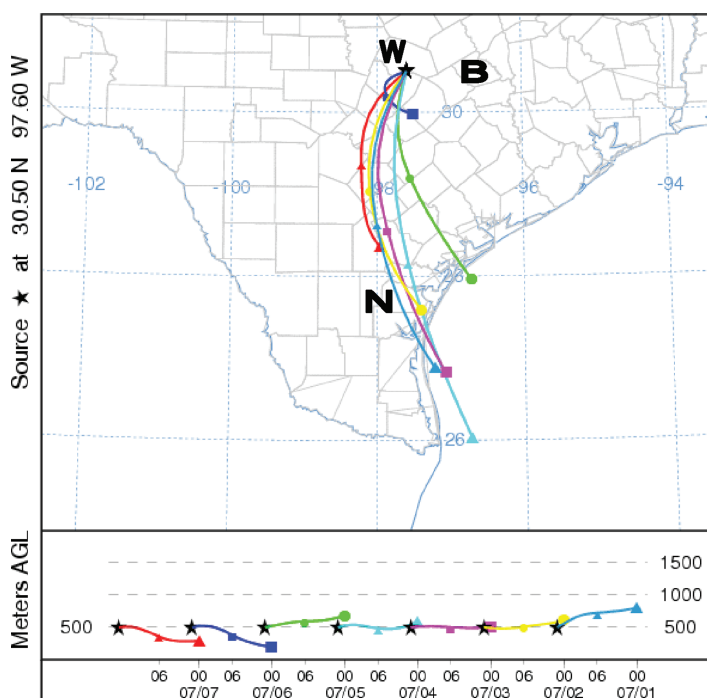


Fig. 4. Backward wind trajectories ending at 12 UTC (0900 hours local time) for 7 July 2005 (first trajectory on left in bottom panel) through 1 July 2005 (last trajectory in bottom panel) in reverse chronological order. B, Burleson Co. (Brazos Valley); N, Nueces Co. (Coastal Bend); W, Williamson Co. (Blackland Prairies). Star on map represents the area where the wind trajectories from the Coastal Bend recorded for the previous 12 h ended, in Williamson County.

the 2003 population was significantly higher than both ( $LC_{50}$  95% CI of the 2003/2005 ratio = 1.07–5.0; 95% CI of the 2003/2006 ratio = 1.27–7.58). No

significant differences were found for the  $LC_{90}$  contrasts (95% CI of the 2003/2005 ratio = 0.21–1.82; 95% CI of the 2003/2006 ratio = 0.28–2.92). Popu-

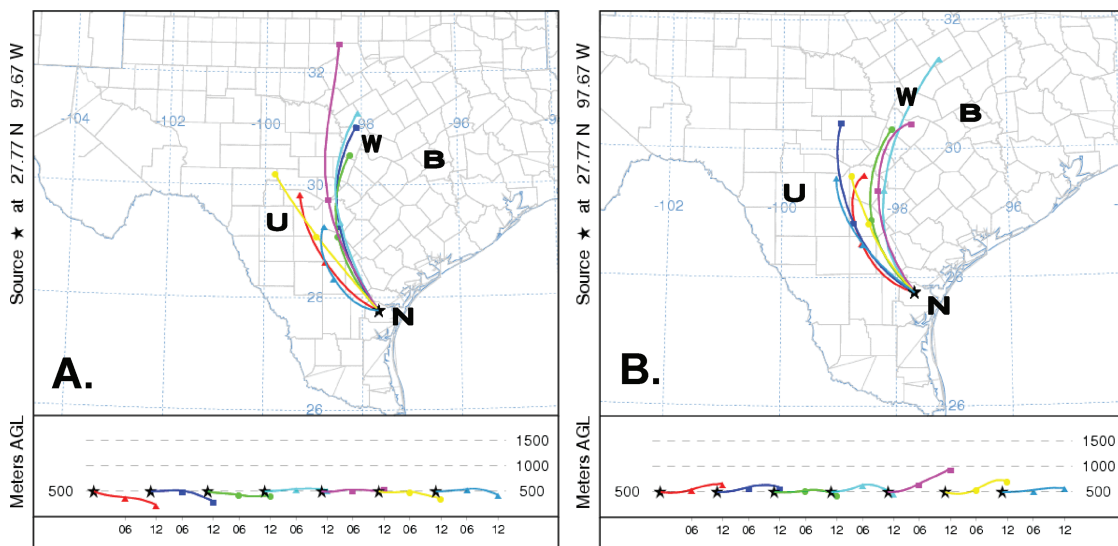


Fig. 5. Forward wind trajectories originating in Nueces County (star). B, Burleson Co. (Brazos Valley); N, Nueces Co. (Coastal Bend); U, Uvalde Co. (Winter Garden); W, Williamson Co. (Blackland Prairies). After 12 h, the wind trajectories ended north and west of the origin, closer to Williamson Co. than to Burleson County. (A) Trajectories starting at 00 UTC on 30 June 2005 (2100 hours local time on 29 June 2005; first trajectory in bottom panel). (B) Trajectories starting at 00 UTC on 23 July 2005 (2100 hours local time on 22 July 2005; first trajectory in bottom panel). Similar wind trajectories were observed for the week of 19 May 2005 and 3 June 2005 (data not shown).

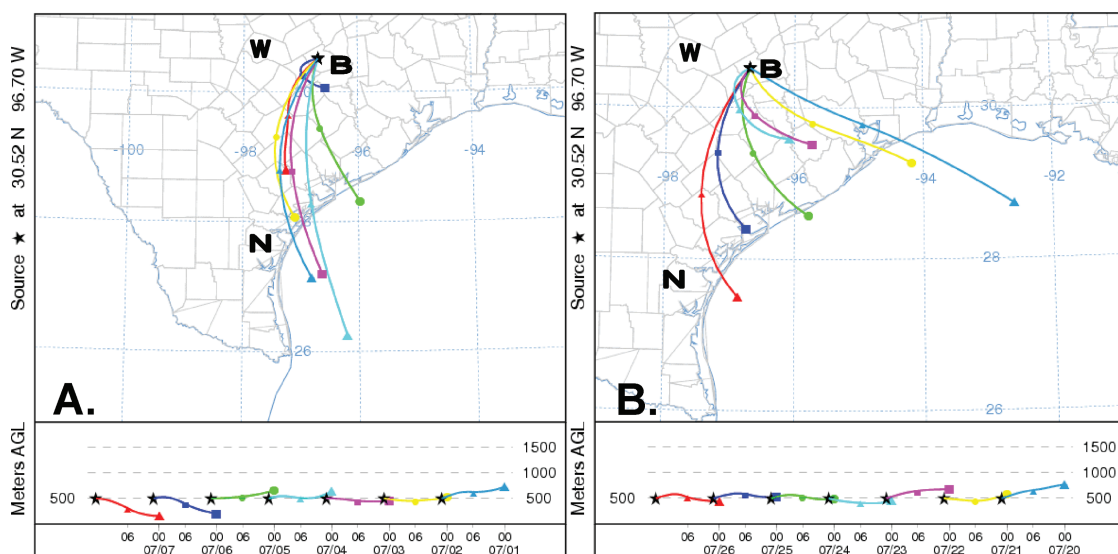


Fig. 6. Backward wind trajectories that have Burleson County as the destination (star). B, Burleson Co. (Brazos Valley); N, Nueces Co. (Coastal Bend); W, Williamson Co. (Blackland Prairies). (A) Trajectories ending at 12 UTC (0900 hours local time) on 7 July 2005. (B) Trajectories ending at 12 UTC (0900 hours local time) on 26 July 2005. Wind trajectories originate in the upper coastal region, north of Nueces County.

lations from 2005 and 2006 were equally susceptible (Table 8;  $LC_{50}$  95% CI for August 2005/2006 ratio = 0.52–3.46;  $LC_{90}$  95% CI for August 2005/2006 ratio = 0.38–5.34). A more detailed analysis of the 2006

season showed that this bollworm population had  $LC_{50}$  values similar to the reference susceptible Burleson Co. population, and susceptibility was maintained throughout the season (Table 9).

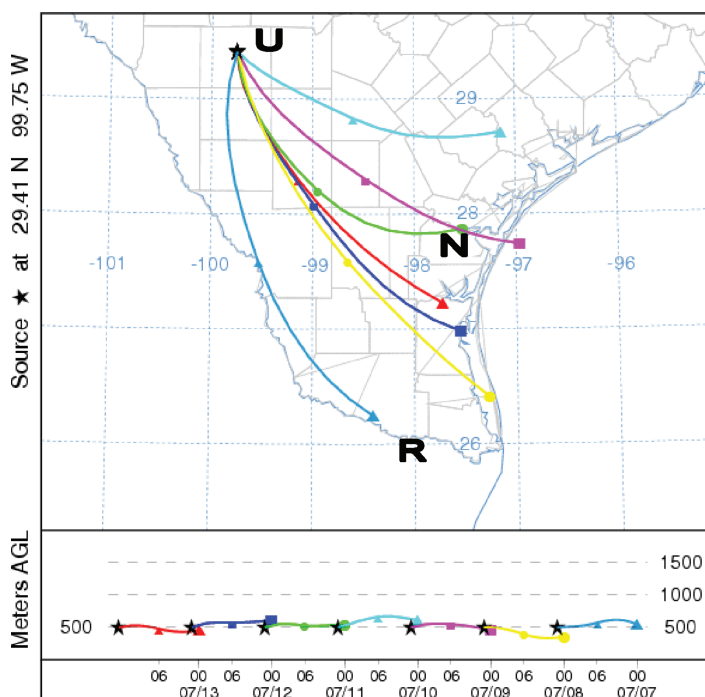


Fig. 7. Backward wind trajectories ending at 12 UTC (0900 hours local time) on 13 July 2005. N, Nueces Co. (Coastal Bend); R, Rio Bravo (Mexico); U, Uvalde Co. (Winter Garden). Star represents the destination point where the wind trajectories from the Coastal Bend and the Rio Grande area ended, in Uvalde County, Winter Garden region.

Table 10. Bollworm resistance allele frequencies ( $q$ ) 2000, 2003–2006

Location	Date	SDD <sup>a</sup> = 3 $\mu$ g/vial	SDD <sup>a</sup> = 5 $\mu$ g/vial	HDD <sup>b</sup> = 10 $\mu$ g/vial
Brazos Valley, Burleson Co.	July 2000	0.342	Not tested at 5 $\mu$ g	0.397
	July 2003	0.280	0.217	0.378
	July 2004	0.174	0.105	0.216
Coastal Bend, Nueces Co.	July 2003	0.289	0.200	0.333 <sup>c</sup>
	July 2004	0.387	0.362	0.524
	July 2005	0.289	0.263	0.459
Coastal Bend, Nueces Co. 2006	May 5–11, 2006	0.338	0.175	0.328
	June 6–18, 2006	0.298	0.219	0.266
	July 1–5, 2006	0.275	0.175	0.223 <sup>c</sup>
	July 18–20, 2006	0.285	0.143	0.327
	Sept. 11, 2006	0.283	0.183	0.258
Blackland Prairies, Williamson Co.	July 2004	0.229	0.148	0.284
	July 2005	0.428	0.393	0.597
Winter Garden, Uvalde Co.	Aug. 2004	0.208	0.166	0.288
	July 2005	0.330	0.230 <sup>d</sup>	0.479
High Plains, Hockley Co.	Aug. 2003	0.148	0.092	0.192
	Aug. 2005	0.150	0.100	0.223

Burleson Co.: for July 2005, no survivors above 3  $\mu$ g/vial; for July 2006, no survivors above 5  $\mu$ g/vial. Williamson Co.: for 2003, no survivors above the 3  $\mu$ g/vial. Hockley Co.: for 2004, no survivors above the 3  $\mu$ g/vial; for Aug. 2006, no survivors above 5  $\mu$ g/vial.

<sup>a</sup> Susceptible discriminatory dosage.

<sup>b</sup> Heterozygote discriminatory dosage.

<sup>c</sup> For July 2003,  $q$  was calculated based on the percentage surviving the 30  $\mu$ g/vial because there were no survivors at 10  $\mu$ g/vial.

<sup>d</sup> Survival at 5  $\mu$ g/vial same as at 10  $\mu$ g/vial.

**Resistance Frequencies.** For all bioassays performed, calculation of the resistant allele ( $q$ ) frequencies showed that the use of 3  $\mu$ g/vial as a discriminatory dosage provided  $q$  values that were similar for the two calculation methods described (nonsignificant  $\chi^2$  tests, data not shown; Table 10). With respect to discriminatory dosage,  $\chi^2$  tests indicated similar  $q$  values between frequencies calculated with either 3 or 5  $\mu$ g/vial; however, the 5- $\mu$ g/vial consideration would overestimate the frequency of susceptible individuals. Therefore, at least for Texas populations, the 3- $\mu$ g/vial discriminatory dosage is preferred because it provides a more conservative estimate of the frequency of susceptible individuals, and it is closer to the originally recommended discriminatory dosage of 2.5  $\mu$ g/vial (Kanga et al. 1996).

## Discussion

The statewide cypermethrin resistance monitoring program for bollworm populations was concentrated in the ecologically diverse cotton production areas in Texas (Fig. 1). Variation in the characteristics of the cotton production regions, as well as the local diversity in agricultural systems, makes the analysis of bollworm resistance development extremely complex. Toxicological bioassays for 2000 and 2003–2006 indicated a varied and problematic situation for pyrethroid use in Texas. The widespread resistance to pyrethroids by bollworm populations could lead to reduced yields and higher production costs and insecticide use in cotton. The development of resistance can also affect crops such as soybeans and sorghum, where the bollworm can be an economic pest, and pyrethroids are the least expensive control tactic (Peters et al. 2005).

Kanga et al. (1996) suggested that if only one concentration of cypermethrin was used for resistance monitoring for male bollworm populations, 2.5  $\mu$ g/vial

would be recommended because all susceptible insects would die, and some resistant insects would survive. This was determined by collecting adults from the field in June and September 1988 in Burleson Co. (Brazos Valley), when susceptibility was high. These insects had a LC<sub>50</sub> of 0.05 and LC<sub>90</sub> of 0.57  $\mu$ g/vial. A clear indication of the high level of resistance in Texas is that many of the populations that we tested exhibited LC<sub>50</sub> values higher than the discriminatory LC<sub>99</sub> dosage of 2.5  $\mu$ g/vial (Tables 1, 3, 4, and 6). The LC<sub>90</sub> ratios calculated for all areas of Texas used the Burleson Co. September 2005 LC<sub>90</sub> of 2.44  $\mu$ g/vial, which is almost identical to the recommended 2.5- $\mu$ g/vial concentration that killed all susceptible insects (Kanga et al. 1996). Therefore, these ratios accurately reflect the level of resistance for the years of this study.

The observation that the  $q$  values were similar between the two methods for most areas suggests that only one major allele is responsible for resistance (Plapp et al. 1990). The molecular mechanism(s) for *H. zea* pyrethroid resistance have not yet been studied for Texas. In addition to the target site insensitivity resistance mechanism (Ottea and Holloway 1998), cytochrome P450 enzymes, CYP321A1 and CYP6B8, have been associated with cypermethrin metabolism in *H. zea* (Li et al. 2004, Sasabe et al. 2004).

Atmospheric trajectory analysis has revealed high frequency of prevailing winds available to transport migrating *H. zea* from one specific crop production region to another, although shifting wind caused by transient mid-latitude weather systems can temporarily alter the potential displacement route. The propensity of *H. zea* to migrate in various headings of prevailing wind has been studied (Wolf et al. 1995) but requires further research. The influence of migrating moths according to predominant wind patterns must be overlaid in the analysis of resistance detection, localization, and evolution and for the development of

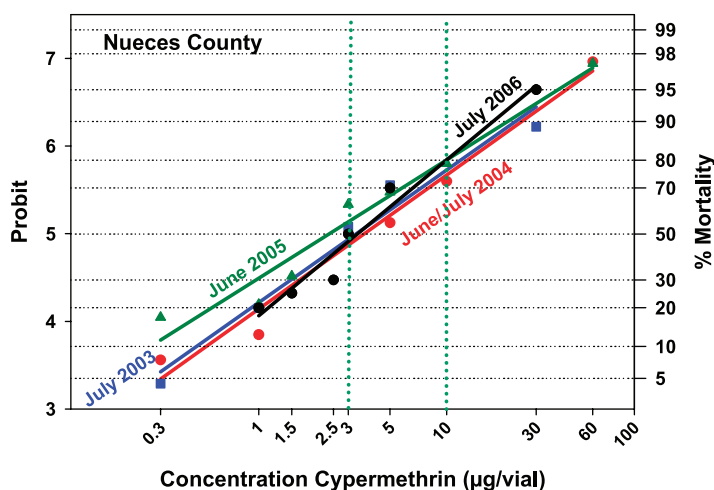


Fig. 8. Probit analysis for male bollworm field-collected during mid season from 2003 to 2006 in Nueces County and exposed to cypermethrin coated vials for 24 h. Lines are statistically equal and parallel ( $P \leq 0.05$ ). The dotted vertical lines indicate the discriminatory doses for susceptible moths ( $<3 \mu\text{g}$  cypermethrin/vial) and heterozygote resistant moths ( $<10 \mu\text{g}$  cypermethrin/vial). Notice that, since 2003, about one half of the population is resistant.

resistance management strategies (Sandstrom et al. 2005). Immigration of resistant moths from regions with higher frequencies of resistant individuals can result in lower pyrethroid effectiveness, even in populations without previous local pyrethroid use or exposure (Caprio and Tabashnik 1992, Croft and Dunley 1993).

**Brazos Valley.** In Burleson Co., the highest cypermethrin resistance ratios were typically observed in July (Table 1). These ratios decreased toward the end of the cotton season, August or September, depending on the year (Pietrantonio et al. 2004, 2005). This seasonality is exemplified by the 2006 data (Table 2). The regression toward susceptibility observed in 2005 in Burleson Co. (Table 1) suggests that alternating compounds with different modes of action and using higher rates of pyrethroids when resistance is in high frequency can aid in eliminating pyrethroid-resistant heterozygote individuals in the population. These practices have been repeatedly recommended to consultants and growers at several local and regional conferences.

**Coastal Bend.** Resistant populations in Nueces Co. exhibited the highest resistance ratios at midseason for both the  $\text{LC}_{50}$  and the  $\text{LC}_{90}$  of all areas tested, and these ratios remained high in the last 4 years (Table 3). There were also a higher number of moths surviving above  $10 \mu\text{g}/\text{vial}$ , likely homozygote resistant, than the percentage of putative heterozygotes, which survived between 3 and  $10 \mu\text{g}/\text{vial}$  (Fig. 8). This means that the high resistance ratios at the peak of resistance in midseason in Nueces Co. for 2004 and 2005 (Table 3) suggests higher numbers of homozygote insects in the population versus any other region assessed (Fig. 8). This is also the only region from which individual insects surviving the highest concentration of  $60 \mu\text{g}$  cypermethrin/vial were detected in 2004 and 2005 (Fig. 8).

In 2005, the surface area of cotton was 95,175 ha in the six counties of the lower Coastal Bend (including

Nueces Co.); 30% were *Bt* cotton. Sorghum surface area in the same region was higher, 182,250 ha, and there were 20,250 ha of corn. It is a common practice of growers in this region to use low rates of pyrethroids in sorghum for control of the sorghum midge, *Contarinia sorghicola* (Coquillett) (Diptera: Cecidomyiidae), when *H. zea* may not be a target pest. This bollworm pyrethroid exposure occurs before its movement into cotton, where additional pyrethroid selection takes place (Fitt and Cotter 2005, Peters et al. 2005). *H. zea* and fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), infestations in sorghum in 2005 were similar to those in 2004 that persisted for a long period, with  $\approx 80\%$  of the sorghum hectares treated in both years. In 2005, no field control failure was reported for *H. zea* in sorghum, with medium to high rates of pyrethroids, nor at that time were problems experienced in cotton. About 2–3 wk after the sorghum treatments, problems controlling *H. zea* in cotton were experienced, but control was achieved with emamectin benzoate (Denim) or indoxacarb (Steward) alone or in mixtures with pyrethroids (Pietrantonio et al., 2006). We speculated that these early pyrethroid treatments against *H. zea* on sorghum relate to increased difficulty in controlling bollworm later in cotton. The observed control field failures were consistent with the high  $\text{LC}_{90}$  resistance ratios observed for the last 4 yr.

In 2003 and 2005, the frequency of susceptible moths increased toward the end of the season in Nueces and Burleson Counties, after pyrethroid selection pressure subsided (Pietrantonio et al. 2004, 2006). We hypothesized that this reflected a potential fitness cost of the resistance allele in the absence of pyrethroid selection. Decreased fitness could also explain why populations at the beginning of 2005 were more susceptible than at the end of 2004 in Nueces and Burleson Counties. In 2006, however, higher resistance ratios were registered earlier,



in May in Nueces Co., before high pyrethroid pressure had taken place, which casts doubt on the putative current fitness cost of the resistance allele. This is supported by mathematical modeling when assuming a partially recessive gene for pyrethroid resistance in bollworm. Relative fitness estimates indicated that, in the absence of pyrethroid selection pressure, there was no fitness cost of the resistance allele (Livingston et al. 2002). The available information seems to point toward local maintenance of resistant populations in Nueces Co., most likely originating in sorghum. Bollworm larvae have a competitive advantage feeding on sorghum versus soybean or cotton (Gore et al. 2003b), and in Nueces Co., they were exposed to sublethal pyrethroid concentrations, perhaps increasing the likelihood of heterozygote survival.

**Blackland Prairies.** In Williamson Co. there was a rapid loss of pyrethroid efficacy in bollworm populations from 2003 to 2005 (Table 6), and producers avoided pyrethroid use in 2005. Therefore, the resistance ratios for the  $LC_{50}$  of 7.6–14.1 (Table 6) explain the field operational control problems that were observed. As in Burleson Co., the majority of cotton is *Bt*, with the exception of the required refuge, but this county has a much higher surface dedicated to grain sorghum,  $\approx 1:1$  ratio with respect to the cotton area. For example, in 2004, there were 14,580 ha of sorghum and 11,745 ha of cotton, and in 2005, there were 12,150 ha of sorghum and 12,960 ha of cotton (Pietrantonio et al. 2005, 2006). The higher densities of moths emerging from sorghum and potential migration from the Coastal Bend, supported by the wind trajectory analysis (Fig. 5B), may partially explain the high resistance ratio of these populations.

**Winter Garden.** The probit lines for Uvalde Co. were statistically similar in 2004 and 2005, and individuals surviving the 10- $\mu$ g cypermethrin/vial dosage were detected from 2004 to 2006 (data not shown). In 2004, some producers reported limited pyrethroid failures of *H. zea* control in Bollgard cotton (Pietrantonio et al. 2005), and in 2005, perhaps because population densities were lower than in 2003 and 2004, no control problems were reported, despite the high resistance ratios. Potential migration of resistant moths from Nueces Co. and/or northeastern Mexico, supported by the wind trajectory analysis, should be considered when designing management plans for the Winter Garden region.

**High Plains.** In the High Plains, although populations are considered susceptible, monitoring should continue, because moths surviving the 10- $\mu$ g cypermethrin/vial dosage were detected in 2003 and 2005. Pyrethroid tolerance was reported in Missouri bollworm populations in regions where no pyrethroids were used, and immigration of resistant moths was cited as the causal factor (Sorenson et al. 1998). This is important when interpreting resistance monitoring data for north Texas where the first moths captured in the season are thought to be southern migrants (Rummel et al. 1986). It is desirable to maintain pyrethroid susceptibility in the High Plains of Texas, because fall reverse migration of bollworms toward south Texas (Pair et al. 1987) may aid in diluting the resistance pool and contribute to pyrethroid use sustainability.

**Conclusion.** Analysis of wind trajectories at mid-season from 2003 to 2006 were consistent and similar to the ones shown here for all areas. This is significant because mid-season coincides with the highest seasonal resistance ratios observed. In summary, the evolution of pyrethroid resistance in *H. zea* in Texas exemplifies that migration may have an important role in the development of resistant populations and that analysis of wind trajectories may aid in explaining differential patterns of resistance development between geographically close areas, which otherwise could not be explained by land or pesticide use.

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